XII.—*On the Coloration of the Mouths and Eggs of Birds.*—I. *The Mouths of Birds.* By C. F. M. Swynnerton, F.L.S., F.E.S., C.M.B.O.U.

(Plate VII.* and text-figure 6.)

1. Introductory.

When I was in England in 1908, my old friend Mr. G. A. K. Marshall, regarding the accepted views on mimicry in insects as in some ways unsatisfactory, urged me to carry out, on my return to Africa, a long and critical series of experiments and special observations to test the validity of those views, as also of the various objections that had from time to time been levelled against them: to try to find out, in short, what really does occur in nature.

In the course of this investigation, which continued through several years, but was at first mainly concerned with insects and the food of insectivorous birds, one very interesting fact in particular came to light. It was unexpected, and at first even unwelcome, for it clashed with my preconceived view that most prey was "palatable." I will describe it below. Once accepted—and my animals forced it on me—it suggested a good contributory explanation for distinctive coloration, and, by doing so, induced me, amongst other things, to experiment in the preferences of bird- and egg-eating animals.

I have given in detail a large number of my experiments, including nearly all those on carnivorous animals, in a paper read before the Linnean Society on the 15th of April, 1915. I there discussed the question of the reliability of such experimentation as I shall describe in this paper, touching on every objection which, to my knowledge, had been brought against it, and stating the measures adopted to render the experiments as reliable as possible. I also made a preliminary statement of the bearing of my results

* For explanation of the Plate, see p. 293.

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generally on the problems and generally-accepted theories of animal coloration.

All I will do here, therefore, is, first to give a brief description of such few of these theories, and of my own results, as bear more especially on the appearance of the eggs and mouths of birds: this to avoid misunderstanding; and to discuss the explanation of the problems that their appearance presents; and, secondly, to describe in detail my experiments on some egg-eating animals. I hope in a later paper to give a fuller account of some of the other results and to discuss their bearing on the coloration of adult birds.

I take this opportunity to thank very warmly Mr. D. P. J. Odendaal, who helped to procure the eggs used in experiment; Mr. H. M. Wallis, who since I first stated my results at the April meeting of the B. O. C. has sent me much information of a most interesting character; and, for their kind permission to work at the eggs in their respective museums and their help while I was doing so, Mr. W. R. Ogilvie-Grant, Lord Rothschild and Dr. Hartert, Dr. Péringuey (Cape Town), Mr. F. W. Fitzsimons (Port Elizabeth), and Mr. E. C. Chubb (Durban). To no one am I more indebted than to Mr. G. A. Boulenger, who, while I was working at my nestlings in the Natural History Museum, placed every facility afforded by the Reptile-room at my disposal, and helped me much with information and suggestions.

2. Theories and Results referred to later.

Concealing or procryptic coloration, with some beautiful illustrations amongst birds, their nestlings and their eggs, is, nevertheless, not worth going into here, except to draw attention to the fact that, where a second, inner, surface is available for exposure, concealing coloration often forms a shield under which the most conspicuous warning (or other) coloration is developed and safely carried by animals whose unpleasantness to enemies is not so marked that they

can carry bright colour always exposed. The procryptic mantle is retained in these cases till detection becomes inevitable. Then it is dropped, and the hidden coloration revealed as a vivid last appeal to the enemy's memory. The young bird's mouth-colours when he opens his bill to an approacher, the coloration of the eggs when the nest is looked into, a butterfly's upper surface during motion, displays by animals fleeing or at bay, illustrate the principle.

Warning Coloration.—Originally his suggestion to Darwin in explanation of the "splendid" coloration of certain caterpillars, Wallace soon extended the idea of "warning" to the colours of numerous other animals, terrestrial and marine. "The animals in question are either the possessors of some deadly weapons, as stings or poison-fangs, or they are uneatable, and are thus so disagreeable to the usual enemies of their kind, that they are never attacked when their peculiar powers or properties are known. . . . . They require [however] some signal or danger-flag which shall serve as a warning to would-be enemies not to attack them, and they have usually obtained this in the form of conspicuous or brilliant coloration."* "Thus the most gaudy colours would be serviceable and might have been gained by variation and the survival of the most easily-recognised individuals" (Darwin, 'The Descent of Man,' 1901 ed. p. 499).

"Deadliness" and absolute "inedibility" are rare qualities even in the unpleasantest of prey, and (as Prof. Poulton's experiments on the lizard, *Phrynocephalus mystaceus*, first indicated) the latter enjoys only a *relative* immunity from attack even when known, for the digestive secretions of a really hungry enemy can, and do, conquer much. Other modifications, too, can be suggested, but the principle of "warning" stands, backed now by much evidence.

The keen study of insect coloration that has taken place under Prof. Poulton's inspiring leadership, has secured an ample recognition of that principle by entomologists, and Mr. R. I. Pocock has made some very interesting suggestions

* Wallace, 'Darwinism,' p. 232.

with regard to its occurrence in mammals. In birds, Mr. G. A. K. Marshall carried out actual experiments with a Mongoose in 1900. This animal (Trans. Ent. Soc. iii. 1902, p. 378) refused "emphatically" an Owl, a Kestrel, a Buff-backed Egret, a Hobby, and a Drongo, but ate a Turtle-Dove, a Standard-wing Nightjar, a Dwarf Goose (*Nettopus*), a Moor-hen, and a Wheatear. "Its dislike of the smell of the Drongo was very marked, especially as it was hungry at the time . . . . .; it made one or two attempts to eat the meat, but finally gave it up. In the case of this bird and the Egret, we would therefore seem to have a case of true warning coloration. This is also probably the case with the Wood-Hoopoes (*Irrisor* and *Rhinopomastus*), which are very conspicuous both in voice and colour" . . . and "both of which emit a strong unpleasant smell . . . . Another bird which has well-known distasteful qualities is the Ground Hornbill (*Bucorax cafer*)." Prof. Poulton had suggested previously ('Colours of Animals,' p. 159), that "the gaudy and strongly-contrasted colours of certain tropical species may be of warning significance."

Conspicousness has always been regarded as of the essence of warning coloration. "Warning colours can be distinguished by the subordination of every other feature to that of conspicuousness. Crude patterns and startlingly contrasted colours are eminently characteristic of a warning appearance" ('Colours of Animals'). Nauseous animals of dull coloration have been regarded as lacking warning coloration. But recent results suggest that, while it may be convenient to thus restrict the term "warning" to those cases of startling conspicuousness which the word so well suggests, the *principle* comes in wherever unpleasant qualities are present, however dull the colouring. It is the *distinctive* element in an unacceptable animal's coloration that enables an enemy to differentiate it from an animal he is hungry enough for. Distinctiveness may be present even in concealing coloration, where it serves for the animal's identification when the latter element has failed to avert its detection. Conspicuousness is purely an auxiliary quality, though a

most useful one, and likely to be selected wherever that is possible, for impressing the enemy's memory and facilitating recognition, and for differentiating a nauseous animal the more strongly from those numerous species that have to depend instead on inconspicuousness for safety.

Distinctive Coloration.—This was explained by Wallace as having come about in response to the necessity for recognition by members of the same species, and "the wonderful diversity of colour and of marking that prevails, especially in birds and insects," was ascribed "to the fact that one of the first needs of a new species would be, to keep separate from its nearest allies, and this could be most readily done by some easily seen external mark of difference" ('Darwinism,' 1889, p. 218).

No one who has studied animals in the field from this point of view, can have failed to observe that Wallace was right, so far as birds were concerned, in attaching the very highest importance to the above factor. I could myself adduce numerous and striking instances of the use of their distinctive colouring and distinctive call-notes and displays by birds of the same species for keeping in touch, for joining up when widely separated and with numerous birds of other species in between, and for recognition generally.

That yet another factor besides this, and besides sexual selection, may, nevertheless, have contributed to the production of distinctiveness and diversity in the appearance even of adult birds and have been, perhaps, mainly responsible for it in certain other directions, is rendered likely by the results of my food-preference experiments. Using insects as prey, I found, whatever vertebrate enemy I employed, that not only would it at a given moment emphatically and persistently refuse some insects, while readily eating others, but that the finest gradation occurred between those species (grade Z, let us call them) that it would eat only under stress of hunger, through grades Y, X, W, V, &c., refused in turn as it gradually "filled up," to the very few species (grade A), that it would regularly eat at all stages, right up to repletion point.

This was found to be as true in relation to wild birds as to captives. Was it also true of the birds themselves, regarded as prey? I experimented fairly exhaustively with more than a hundred species of birds on a cat, a lemur, and (less fully) an owl and a butcher-bird. In view of the relative size of the prey, I did not expect to find the "grading" at all fine; yet it was. Using meat-scraps from the different species, I found, as in the other case, every gradation from Z, only eaten when the animal was exceedingly hungry, right up through all the levels of growing repletion to A, accepted at all times up to repletion. Substituting the whole bird for the scrap of its meat, the same thing would occur. If the animal had refused the meat-scrap it would refuse the whole bird too. If it were easily hungry enough for the scrap, it would commonly tackle the bird itself, and might, appetite growing with eating, go on to make a full meal off it; yet, if it had been offered the same bird when only slightly fuller, it might have refused it absolutely. It was evidently a matter of relative digestibility and varying digestive power, a flow of the digestive secretions being stimulated when the stomach was empty by objects that were untempting, or even, as experiment showed, definitely inhibitive on a somewhat fuller stomach.

Obviously, if the above be the general rule (and I have so far found no exceptions to it), there can be relatively few species of animals that will not sometimes require to be distinguished by an enemy not hungry enough for themselves, from species (including, often, it may be, their own parent form) that he *is* hungry enough for. This suggests the contributory explanation for distinctiveness and diversity that I have referred to above. The necessity for differentiation from a pleasanter parent form will have been not the least important consideration, for unless correlated with some new distinctive character, a variation in the direction of increased unpleasantness will hardly have been selected. The cumulative action of this need for differentiation, where oft-repeated in the history of a species, might even be invoked to assist in the explanation of certain cases of

apparently exaggerated conspicuousness or elaboration of ornament.

To sum up :—

Distinctiveness and conspicuousness will, in the main, though by no means exclusively, have been selected in relation to the need for recognition, (1) by friends, (2) by enemies ; and *both* these factors will very commonly have contributed to the production of the distinctive characteristics of even a single species. I refer not only to distinctiveness of appearance, but to any characteristics—call-notes, smells, displays, &c.—that may be useful for differentiation by either friends or enemies.

"*Mimicry*" : *special protective resemblance*.—Special resemblances, both to other animals and to particular inanimate objects, were much noticed and written of at a quite early date, the first recorded case being Aristotle's of the resemblance of a cuckoo to a hawk. But the first author who definitely applied to them a selectionist interpretation, only four years after Darwin and Wallace's famous joint essay, was H. W. Bates, of Amazons fame. In his classical paper, "Contributions to an Insect Fauna of the Amazons Valley" (Trans. Linn. Soc. xxiii. pt. iii. 1862, p. 495), he enumerates cases of resemblance both to inanimate objects and to unrelated animals, links them by means of a longicorn group, some of the members of which resemble the former, some the latter, and claims the same principle for both. Moreover he maintains that in a day-flying moth resembling a wasp, the resemblance is "to protect the otherwise defenceless insect by deceiving insectivorous birds," and suggests that, in butterflies, the "mimicry" of the Heliconidæ by *Leptalis* is analogous to this, only that where the wasp is avoided for its sting, the Heliconidæ, with a peculiar smell, abundant, and never seen to be attacked, "are unpalatable to insect enemies." He mentions "two instances of mimicry in birds .... communicated to me by my old travelling-companion, Mr. A. R. Wallace" (the now classical case of *Philemon* and *Mimeta*); and he suggests natural selection

as having brought about the resemblances, "the less perfect degrees of resemblance being, generation after generation, eliminated" by enemies that failed to be deceived.

There was, however, one class of case that still puzzled Bates. The mimicry of an unpalatable animal by a palatable one was easily explained. But equally good resemblances occurred where both "model" and "mimic" were unpalatable! Some of these, he thought, must be the effect of a similar environment acting on organisms related by affinity and already alike. Others, he apparently felt, were real cases of mimicry*, though, as both parties to the resemblance were unpalatable, he confessed himself unable to suggest the additional advantage, possessed by the "model" alone. It is in virtue of this that the members of the genus *Napeogenes*, for example, had come to mimic abundant and flourishing, and therefore presumably less persecuted, species of the Ithomiæ. Evidently the idea of varying *degrees* of unpleasantness failed to strike him (as it also failed to strike Müller); evidently, too, the advantage of sharing in the *notoriety* of the more abundant form, to avoid the numerous mistaken attacks that fall on a little-known species, did not occur to him.

Fritz Müller, writing in 'Kosmos' in May 1879, tried to solve the difficulty. He suggested that young animals, in sampling the qualities of unpalatable species, probably destroy about an equal number of the members of each such species with a separate colour-pattern, before learning to leave them alone altogether. It would follow that a scarce species, while losing the same absolute number of individuals from this cause, would lose a far higher percentage than an abundant one, and might profitably, therefore, mimic the latter. Again, it would be advantageous for two equally unpleasant and abundant species to adopt the same coloration, as, sharing the loss, each would now lose only

* As I read him: Prof. Poulton, however, doubts whether, in spite of his use of the word mimicry, Bates really regarded these cases as such.

one half of what it lost when their colour-patterns were different. This is, of course, what is known as "Müllerian mimicry," "common warning colours," or "synaposematism."

I have myself made a point of testing very fully indeed the validity of both theories. I found, in common with previous experimenters, that Bates was right in supposing that some species are pleasant and others unpleasant (it is a matter of relative digestibility rather than of "unpalatability"). But I also found—as Marshall had begun to find—that there were numerous *degrees* of unpleasantness. This at once extends Bates' principle even to the class of resemblance—that between unpleasant species—which had so puzzled him. I found moreover that Müller was wrong in supposing that after a certain number of tastings, approximately the same for each different appearance, young birds refrain from attack on unpleasant prey. Birds go on all their lives eating such prey whenever hungry enough—it may be several times a day—and, moreover, they go on all their lives making mistaken attacks, though these mistakes are less frequent apparently in the case of prey that they have frequently and recently met with.

From this last, it would seem to be true enough that an abundant species may be less persecuted than a scarce one with a different colour-pattern. But this comes about not in virtue of its incurring the same absolute loss as the other, as Müller supposed, but through a quite different principle—greater reminding-power and far less attack.

In this case, again, it may pay two species with the same unpleasant qualities to possess a colour-link in common, not in order to share between them a fixed and otherwise irreducible loss, but for greater reminding-power and facilitated recognition generally, resulting in lessened attack. This is "synaposematism" as it probably actually exists.

To sum up: (1) A pleasant species may mimic an unpleasant species and so share in its relative immunity from

legitimate attack—mimicry for shelter, one might say. (2) A less-known unpleasant species may mimic an abundant, well-known species, and so share in its relative immunity from *mistaken* attack—mimicry for due notoriety. Or, (3) conceivedly, two abundant and unpleasant species may develop points of resemblance to one another, such as will associate them, to their mutual advantage, in an enemy's mind—mimicry for *increased* notoriety.

Mimicry is best regarded, perhaps, not as of different kinds but simply as mimicry, with the above as factors contributing to each particular instance in varying and not always easily-ascertainable proportions. For most mimics have some unpleasantness of their own, and there are probably few models that are not to some extent more unpleasant than their mimic, as well as more abundant. But, however they are built up, the function of many common groups to-day is, I believe, largely a matter of memory and simplification.

3. On the Mouth-colours of Nestlings.

Towards the end of 1908, I was much struck by the mouth-markings of a brood of nestling *Estrilda astrild*. The possibility that both the pattern and the distinctive hissing sound uttered by the young birds might be of a "warning" nature—a reminder to enemies of the presence of some degree of nauseousness—at once occurred to me. I therefore made a coloured drawing of a mouth of one of the nestlings (Pl. VII. fig. 7), and resolved to follow up the observation by others. *Prinia mystacea* (fig. 8), *Colius striatus minor* (fig. 17), and *Pycnonotus layardi* (figs. 15, 38), were noted soon afterwards; but I shortly became absorbed in other directions, and it was not until late in the breeding-season 1912–13 that the distinctive and striking mouths of some nestling *Macronyx croceus* (figs. 19, 20), *Chloropeta natalensis* (figs. 9, 33), and *Centropus burchelli* (fig. 21), which I was rearing, recalled me to the subject.

The study is an extraordinarily interesting one. The

coloration of the mouths of nestlings is often of so striking and fascinating a character, with its well-marked pattern and its vividness comparable to those of eggs and of butterflies, that it is a matter for real wonder that so little attention has been paid to it. A few cases, such as that of the Gouldian Finch (*Poëphila mirabilis*), have attracted special remark, and led to an attempt at explanation. Mr. Collingwood Ingram, again, has given a summary of a considerable number of interesting observations in his paper "On Tongue-marks in Young Birds" ('Ibis,' 1907, pp. 574–578).

Recently, Mr. Pycraft, in his 'Infancy of Animals,' has discussed fairly fully the "more or less brilliantly-coloured" mouths of nestling Passerines, as also the significance and origin of the "ornaments"; and this is by no means his first or most important contribution to the subject, for the "direction-marking" explanation, undoubtedly applicable in certain cases, is his. But no one, I think, has published so many detailed observations on the subject as that admirable observer, Mr. G. L. Bates, has included in his "Further Notes on the Birds of Southern Cameroon" ('Ibis,' 1911, pp. 581–631). My own observations, mostly long subsequent to his, and all subsequent to Mr. Ingram's, were nevertheless, as accident had it, made independently. I fear it shows how irregularly I have studied my 'Ibis' when absorbed in other work!

Family-characteristics.—One of the first things that strikes the observer is the tendency to similarity between the nestling-mouths of related species. I will take some of the patterns in turn.

1. The twin-spot tongue. Twin spots, vividly black (usually, but in some birds paler), on or close below the two basal spurs of the tongue. Background most usually yellow or orange-yellow, but in some cases (*e.g.* Whitethroat and *Cisticola natalensis*, fig. 6) of some other colour.

The twin-spot tongue is essentially and primarily, I believe, a Warbler characteristic. It is least intense, according to Mr. Ingram, in *Sylvia*, but he has found it in

Palæarctic *Hypolais, Acrocephalus, Locustella, Cisticola*, and *Sylvia*; Mr. Bates describes it for West African *Cisticola erythrops, Calamocichla rufescens, Burnesia bairdi, B. leucopogon, Euprinodes rufogularis, Apalis binotata* (spots dark, not black), *Camaroptera griseoviridis*, and *Sylviella denti*; and I have found it (or in slightly older birds the remains of it) in south-east African *Prinia mystacea* (fig. 8), *Cisticola natalensis* (fig. 6), *C. cinerascens* (fig. 10), *Apalis thoracica, Chlorodyta neglecta*, and the Palæarctic *Sylvia cinerea*. That is, it occurs in all the fourteen genera of the Sylviidæ described by Mr. Ingram or Mr. Bates, or observed by myself. *Locustella* has a third spot, near the tip of the tongue.

2. The "domino" mouth. Symmetrically-arranged black spots on a pale palate. It is present with variations in many, probably most, of the Estrildinæ, such as *Spermospiza guttata, Pytelia nitidula, Poëphila mirabilis, Hypargos schlegeli, Lagonosticta rhodopareia* (figs. 4, 5), *Estrilda astrild, E. nonnula, E. melpoda, E. atricapilla, Nigrita luteifrons*, and *N. fusconota*. All have this mouth, the resemblance between the last six species being apparently particularly close, as also that between the above *Hypargos* (figured by Bates) and the *Lagonosticta* as noted by myself.

3. The plain orange mouth with paler flanges (greenish-yellow mouth in *Tchitrea viridis*) of all the Flycatchers but one described by Mr. Bates—*Fraseria ocreata, Pedilorhynchus comitatus, Erythrocercus maccalli, Trochocercus nigro-mitratus*, and *Tchitrea*. The exception was *Chloropeta* (figs. 9, 33), one that I have myself noted, too, and will refer to again below.

4. Plain yellow to orange, with paler flanges, is the colouring of some, at any rate, of the English thrushes, deeper in the Blackbird, paler in the Mistle-Thrush (fig. 26).

5. The scarlet-lake or crimson mouth with pale yellow flanges of the nestling Weavers of my acquaintance—*Hyphantornis jamesoni* (figs. 13, 18), *H. nigriceps, Sitagra ocularia, Amblyospiza albifrons* (fig. 1), and *Coliuspasser ardens* (figs. 2, 3); also *Pyromelana flammiceps* according to Bates.

6. The only two Doves, the nestling-mouths of which

I have examined, have these in each case dull plain brownish grey or grey-brown. They are *Chalcopelia afra* and *Turtur capicola* (figs. 24, 25).

It is the same when we come down to genera. We have considered some such cases incidentally already. Another is that of *Chloropeta*. The mouth of *C. batesi*, its finder's only aberrant Flycatcher, resembles that of *C. natalensis* (figs. 9, 33). Again, his *Pycnonotus* (*P. gabonensis*) has a white-flanged deep-red mouth. That of *P. layardi* (figs. 15, 38) may not be quite so deep or the flanges quite so white, but the two mouths are evidently not dissimilar. Mr. Bates' description of the mouth of the Green Bulbul (*Phyllostrophus simplex*)—flesh-red, and the swollen margin of the gape pale yellow—is even more like our *Pycnonotus*. His *Colius nigricollis* has a yellow, very conspicuous tongue in a slaty-black mouth, which must, therefore, much resemble that of *Colius striatus minor* (fig. 17). Plain yellow with paler flanges is the mouth of *Cinnyris venustus niassæ* (figs. 22, 23) at Chirinda, and whitish-flanged plain orange was that of Mr. Bates' *Cinnyris minullus*.

These instances might be added to, but they are sufficient to suggest, (1) that most of the resemblances occurring between nestlings' mouths are due to affinity; and (2) that the mouth-patterns of nestlings may, as Mr. Ingram has suggested, "prove of some small taxonomic value." But I would add, they should be used with the caution that coloration always demands. That it is very necessary here is shown by the existence of exceptions.

The two species of *Chloropeta* I have mentioned, "have," in Mr. Bates' words, "the inside of the mouth and the tongue orange, and the tongue has a pair of black spots at the base—a character found in no other nestling Flycatcher." And it is, as we have seen, a Warbler character. Similarly, the Hedge-Sparrow has a Warbler tongue. The English Skylark's tongue (fig. 30), black-tipped, is not unlike that of *Locustella* in its spotting, and the tongues of *Motacilla raii* and *M. lugubris* are, Mr. Ingram tells us, like those of *Sylvia*—or is it that *Sylvia* has varied

in the direction of *Motacilla*? Again, in depending for distinctiveness on the contrast to a dark background of its two bright rows of palatal papillæ, the mouth of *Macronyx croceus* (figs. 19, 20) resembles to that extent the mouth of the Bearded Tit (the actual appearance must be very different owing to its lacking the latter's black patch); yet the two birds are not related. The mouth of *Cisticola cinerascens* (fig. 10) also much more resembles that of *Prinia mystacea* (fig. 8) than it is like that of its own congener, *C. natalensis* (figs. 6, 12), the result of a quite different ground-colour. There is a strong likeness between the mouth-coloration of *Pycnonotus layardi* (figs. 15, 38), *Hyphantornis jamesoni* (figs. 13, 18), and a *Chrysococcyx* (fig. 14), parasitic on the latter, yet no affinity is present. The three Bulbuls already mentioned have a bright or deep flesh-red mouth, yet another, *Phyllostrophus flavigula*, has an orange mouth, and yet another, *Andropadus latirostris*, has it yellow.

Meaning of the distinctive coloration of nestlings' mouths.—The only explanation attempted up to the present, so far as I am aware, has been that of directive markings, on the analogy of the explanation given for certain markings in flowers. Mr. D. Seth-Smith, at the B. O. C. meeting at which I first stated my results, mentioned the semi-luminous, bead-like blue warts which are present on the sides of the base of the mandibles in the nestlings of certain species of birds, such as the Gouldian Grassfinch (*Poëphila mirabilis*) and the Parrot-Finches (*Erythrura*). He remarked that these appeared to be necessary in order to indicate to the parent-birds where to place the food. When feeding, the parent stood in the entrance-hole of the nest, excluding almost all light, and in this position the nestlings were nearly invisible; but when their mouths were opened these could be easily located by the presence of the blue beads, which were placed, as it were, at each corner of a square.

It seems to me exceedingly probable that the function of the blue beads in these and other species is directive, and that usefulness for directive purposes may, at any rate, have

contributed to the selection of special markings or a pale-flanged dark mouth in other cases as well. But as a complete explanation for the whole of the striking phenomena of the coloration of nestlings' mouths the explanation is inadequate, and I am inclined to agree with all that Mr. Ingram says on the subject ('Ibis,' 1907, p. 576).

Thus, the mouth of a Starling (*Lamprocolius splendidus*), which nests in a hole, is described by Mr. Bates ('Ibis,' 1911, p. 542) as follows:—"Flesh-coloured tinged with yellow" with "conspicuous white mouth-flange" and a dark tongue "becoming black at the base." This strikes one as, perhaps, a very perfect instance of what, with variations, we might naturally expect throughout if the "directive marking" view be universally applicable, even the excellent device of luminous points on the outer margin, as described for *Poëphila*, being hardly an improvement on such a mouth. Yet in the English Starling, which also builds in a hole, the mouth remains plain bright yellow, like that of the Mistle-Thrush (fig. 26), the Fiskal Shrike (figs. 16, 47), and a number of other nestlings whose parents lay in open, brilliantly-lit nests. In this case, at any rate, the plainness would appear not to have been of such great detriment as to necessitate the selection of an additional signal for use in holes. And even these plainly pigmented mouths, whether in holes or out of them, require some explanation.

Again, if we admit that in the Warblers which build domed nests, the twin spots at the base of the tongue have been so vitally useful "directively" as to have been selected for that reason alone, while *Sylvia*, taking again to open nests, has begun to have the spots obscured; and if we argue similarly for the white spots of the Bearded Tit (some of the most conspicuous of which, like the third spot of *Locustella*, seem to me to be frankly *mis*-directive). Why, then, is it that *Alauda* (fig. 30), nesting openly on the ground, has adopted the same spots as the Warblers—with the addition, it is true, of three spots as widely misdirective as the length of the tongue and the mandibles will allow? Why has *Macronyx* (figs. 19, 20), nesting openly on the ground, developed the same markings as the Bearded Tit? Is there any really good reason to

suppose that these Larks and Pipits have abandoned the habit of laying in holes or domed nests so relatively recently that the directive (and misdirective?) markings, no longer of real value, have not had time to disappear? Why has the Hedge-Sparrow nestling, lying in an open nest, a mouth even more like a Warbler's? And why has the one Flycatcher that choses to stray from the normal coloration of its kind also adopted directive markings, indistinguishable from those of the Warblers'; while at the same time it continues to use a wide-open nest, built in the most open and brilliantly-lit situation chosen by any Flycatcher that I know, namely (in my experience) on the upper surface of high-placed bracken fronds? And why are the resemblance between the tongues of some of these unrelated birds so nearly exact? Where a plain yellow mouth like the English Starling's, a twin-spot tongue like the Warblers', and a mouth with black spots at the tips of the tongue and mandibles, are each and all directive, or, at any rate, apparently equally successful in getting abundantly fed, what matter to *Accentor* and *Chloropeta* if their mouths should *not* be quite Warbler-like? Of what value, on the view of directive markings, is it to the young *Chrysococcyx* to have a mouth coloured like that of the young of its *Hyphantornis* host? Were it plain yellow, or crimson, or brown (or even with twin spots or "domino" palate, for the nest is domed), would the Weaver foster-parents, unused to all but plain pink, waste time in uncertainty and the young Cuckoo be ill-nourished? *

Some of my questions are, perhaps, not unanswerable, but I have attempted to show that the "directive marking" principle, though doubtless in some cases present and highly useful, will not explain the whole of the phenomena, nor, indeed, does Mr. Pycraft make any such claim. After all, it is nestling mouth-colour generally that wants explaining—its vividness, its distinctiveness, and its fairly considerable

* I have since placed a young Weaver (*Sitagra ocularia*) in the nest of a Flycatcher (*Chloropeta*), and watched its feeding. The Flycatcher seemed to experience no inconvenience whatever from the different mouth-colour and the absence of twin spots, or even from the rapid vibration of the head.

diversity—and not merely certain spots in the mouths of nestlings in holes and domed nests. Such spots are as often as not absent from mouths, which observation in the field shows are often vividly displayed, wide open, in the brilliant light of day through the opening in the nest on the latter being jarred, just as the nestlings in open nests crane their heads and open mouths upwards. The "directive" analogy was from flowers. Nestlings, like flowers, "heliotrope."

Pressing the analogy, I may say that, even in the matter of flowers, it is recognised that the theory of directive markings has sometimes been carried too far. As Kerner and Oliver remark (Nat. Hist. Plants, vol. ii. p. 191):—"It would be too much to say that all spots are to be regarded as signals, or to call them 'honey-indicators' or 'path-finders.'" Markings in flowers are, in very numerous cases, apparently useful only for giving them a distinctive appearance (as, in another case, a plain colour might), whereby they may be the more readily differentiated from the parent form and other species by the pollinating insects, that prefer them to these; and this "distinctiveness for recognition" brings us down to an explanation which I believe to be somewhat widely applicable to the distinctive coloration of nestlings' mouths.

Distinctiveness for ready differentiation by enemies.—I will first quote, for what it may be worth, a conversation with my native trapper, Mandina. It is recorded more fully in my longer paper.

". . . . We went on to discuss nestlings. I said: 'Have the nice birds always nice nestlings, and the less nice birds less nice nestlings?' He said: 'No; nestlings are always far less nice than their parents; the younger they are the unpleasanter they are, and we generally leave them until they are, at any rate, getting their wing-feathers. But even then they are not so nice as when they are beginning to fly, and when beginning to fly they are less nice than when full grown.' I said: 'I know you usually leave young nestlings to fledge before taking them; but is not this to get a bigger meal out of them?' 'Partly,' he

said, 'but they are left for the other reason, too—to get rid of the *Ipunga* (smell or flavour). Of birds that we eat in the adult state we eat the nestlings too, but we like them all less than we do the old birds. Very small nestlings are not eaten at all except by certain people who do not seem to mind the *Ipunga*. It is strongest in newly-hatched birds, and that is the chief reason why we let them remain till the feathers appear.' 'Is this *Ipunga* a taste or a smell?' 'You taste it in the mouth, but you can often smell it, too, in very young nestlings.' . . . ."

In the light of the law of complementation, the idea is probable enough; for a nestling, unable to fly away from its enemies, may well require some slight additional protection beyond numbers and such concealment and defence as the nest and its own appearance and the parent birds may afford. Various young butterfly larvæ (also the eggs) are far less readily attacked by driver ants than when they have grown larger and developed emissible juices or procryptic coloration. The seedling foliage in some groups of plants is more disliked by herbivorous animals than the adult foliage, normally out of their reach. Still, young rooks are excellent eating! So, pending special experiment, I give the view, widely held amongst our natives, merely for what it is worth.

It is, in any case, not required for our purpose. Experimenting, even with adults and somewhat immature birds—in two or three cases with actual nestlings—I found many species that were disliked, and a fine gradation between the best-liked species and the worst, as I have explained above under "Distinctive coloration." Therefore, remembering that nestlings tend to open their mouths wide to all comers, and that, in youngish nestlings especially, the large wide-open mouth is the most visible portion—that, in fact, there is often nothing but mouths visible when all the nestlings crane upwards or outwards together—I would suggest that the distinctive coloration of the mouths of nestlings has, to a large extent, been retained in relation to the necessity for ready differentiation by enemies, or for the differentiation,

by them, of a nestling they are not hungry enough for, from that of such species as they are, at the moment, hungry enough for. It is quite true that an insufficiently hungry enemy may come back when he next is hungry enough, and in the immediate neighbourhood; but the chance has been given to the parent birds to remove their young (and they often take the hint), or even to bring them off in safety before the nest is revisited—as we ourselves, wishing to rear the young birds, sometimes find has happened.

The conspicuousness of many of the mouths, as apart from mere distinguishability, is doubtless of use in impressing their appearance on the enemy's memory and facilitating their recognition when seen again. It is for readier recognition; and the selection and development of this character have thus been rendered possible, in spite of the apparent disadvantage that the result may facilitate detection; for the mouth is only opened and its brilliant colours displayed when the nest is approached and likely to be seen in any case.

Mimicry—for protection or increased notoriety—may help us to account for some of the mouths, though the material is still far too scanty to admit of a positive interpretation.

Take first the Warblers. The twin spots are probably an ancestral character common through affinity to all such Warblers as now possess them. That their retention may have been in part due to their continued usefulness and consequent selection is not, however, impossible. "All the butterfly sub-families, which furnish the chief models for mimicry, are remarkable for the uniformity of colour and pattern throughout groups of species in each of the countries they inhabit. . . . . A very strong family likeness runs through long series of species." * This can be accounted for by the advantage of maintained notoriety. It has not brought about the resemblance—affinity sufficed for that,—but it has tended to prevent divergence. If Warbler nestlings generally are to some slight extent unpleasant to their enemies, their common retention of the characteristic mouth may in the same way have been in part a matter of "common

* Poulton, 'Essays on Evolution,' p. 277.

warning colours." Any additional advantage the twin spots may possess as directive markings would doubtless also have contributed to their retention.

Chloropeta natalensis (figs. 9, 33), a Flycatcher with a very vivid Warbler-like mouth, falls into the same colour-group at Chirinda as *Cisticola cinerascens* (figs. 10, 11) and *Prinia mystacea* (fig. 8), an abundant Warbler that, experimenting with adult and still immature birds, I found to be fairly low-grade—disliked, that is, to a fair extent by the animals I tried it on. The three birds inhabit the same "veld"—grass country interspersed with bracken, low shrubs, &c., and they build at about the same height from the ground, and thus probably possess the same nestling enemies. So that the resemblance, if, as I think, it is advantageous to the Flycatcher, is probably being retained by selection to-day whether it originally arose as mimicry or by coincidence pure and simple, or from the retention of or reversion to a mouth-pattern more ancestral than the present spotless mouth of its relations. The rejection of the present normal colouring might have been associated with the Flycatcher's taking to a new kind of station (as it has done) and so coming in contact with the enemies of the Warblers whose station it had invaded instead of its old enemies, acquainted with the plain orange Flycatcher mouth such as would often be met with in bush country; and its new lack of notoriety might have been the main factor in bringing about the selection of the likeness. At any rate, my experiments with the adult birds do not lead me to suppose that nestling *Chloropeta* is likely to be better liked by enemies than nestling *Prinia*. That *Chloropeta batesi*, of southern Cameroon, should have the same mouth is, in itself, no objection to this view. The resemblance to a yellow-mouthed Warbler may have arisen first in an ancestor of the two species and have continued in themselves through the advantage it still afforded them, much as I suggested for the distinctive mouth of the Warblers.

Resemblances, and particularly resemblances in such simple patterns as we find in birds' mouths, so often arise

quite independently—demonstrably so—that suggestions of mimicry should be made with caution and reserve. Again, someone may some day demonstrate that *Chloropeta* is itself a Warbler! In that case, too, I will gladly withdraw my suggestion.

Or—as I have already practically suggested, and as is exceedingly likely—fuller records may show that the twin-spot tongue is to the mouths of nestlings what the longitudinally-striped pattern is to the down-plumages of young birds—an ancestral character of extremely early date, surviving in a number of now unrelated descendants through the advantages it still continues to offer those particular species or groups of species; not in this case advantages of concealment, but of easy memorability. I am finding the twin spots, since I first wrote this paper, in more and more birds—*Zosterops*, *Erithacus*, *Laniarius*, &c.

Yet another case of homœochromatism is found at Chirinda in the nestling-mouths of *Pycnonotus layardi*, *Hyphantornis jamesoni*, and a *Chrysococcyx*, probably *C. cupreus*, found in the latter's nest (figs. 13–15). Not looking at it carefully, I took it for granted that the young Cuckoo was a Weaver, and continued to do so until after opening its mouth and settling down to draw it. Then I noticed the palate and, looking, found the raised nostrils. *C. cupreus* lays much, I believe, in nests of *Hyphantornis*. Whether its other hosts are as well chosen in the matter of mouth-colour I do not know. Should this prove not to be a mere isolated coincidence, the question might arise whether it might have come about by the discriminative action of enemies or of the parent bird. The latter seems to me more likely to come into play in eggs than in relation to the hatched bird*. The presence of the

* Since writing this I have placed a young *Sitagra ocularia* in the nests of a Rock-Thrush (*Monticola angolensis*) and a Flycatcher (*Chloropeta natalensis*). It was adopted in each case, in spite of its different external appearance, its very different mouth, its extraordinary manner, and its different call-note. The Rock-Thrush had ejected *eggs* not its own—a most interesting and significant fact which I will acknowledge more fully later.

Bulbul in this homœochromatic combination is at first sight interesting, but it would be unsafe to suggest mimicry until more is known of the mouths of Bulbuls and Weavers generally, where geographically associated and where not. I quote from my original note on the bird whose mouth is figured (Pl. VII. fig. 15):—"18.3.13. *Pycnonotus layardi.* Barely beginning to feather. Three in nest, all same. Mouth-likeness to *Hyph. jamesoni* extraordinary, and same wobble of head. Has a rather Weaver-like food-note too, 'tsip, tsee,' as well as a more Bulbul-like tone. . . . . Sometimes brighter than at others, even nearly carmine." I found, in fact, that when I opened the mouth myself it was dull pale brownish in coloration, the bright colour that makes it so like the Weaver's mouth being, in this case, evidently due, not to pigment, but to a rush of blood to the mouth under the stimulus of eagerness. So much at present for resemblances.

Highly distinctive mouths were those of *Colius striatus minor* (fig. 17)—a yellow "lantern" of a fleshy tongue in a black mouth—and, yet more distinctive, *Centropus burchelli* (fig. 21)—tongue crimson and black, with white papillæ (the latter not so conspicuously displayed as in the figure) in an otherwise unpigmented mouth, and with its own terminal third unpigmented. The young birds of *Centropus* had "a remarkable wheezy food-call, uttered continuously when anyone was present, the tongue being pushed rapidly back and forth meantime with mouth wide open and directed straight at the approacher." One of these nestlings that I offered to a lemur and a cat was apparently much disliked by them. A youngish *Trachyphonus cafer* (fig. 44) that I shot still showed strong traces of what seemed to have been a similarly coloured tongue less strongly, as did an *Indicator*, a matter probably of affinity. Yet another rather striking mouth was that of a nestling *Macronyx croceus*, which I have also figured (Pl. VII. fig. 19). I do not know the food-status of this nestling. The eggs were much disliked by my rat, while the adult birds were placed quite high in the scale of palatability, though not amongst the pleasantest, by my cat

and lemur. It may be that the nestling is intermediate. But even a very slightly unpleasant species will, if it be unpleasant at all, derive much advantage from a conspicuous and easily remembered appearance. The only question is, Can it safely carry it—as a highly nauseous species often can? The shut mouth of a young bird is a sufficient shield from this point of view. Being seen, nevertheless, its one remaining chance of averting attack is identification. Hence the distinctive colouring.

It was interesting that both the Doves examined had very dull mouths. Their mode of feeding, and the fact that they do not open their mouths when approached—they cannot to any great extent—had led me to expect this. Young Nightjars, again (in my experience), tend only to open their mouths when they are actually touched—doubtless a part of the procryptic scheme—and their very large canvases remain quite unpainted.

Other distinctive characteristics.—I have referred to the extraordinary tongue-action and wheezing sound of young *Centropus burchelli*, also to the nestling notes of *Pycnonotus layardi* and the extraordinary vibration of the head that the same nestling possesses in common with *Hyphantornis jamesoni*. It is a regular Ploceid character, and it would be interesting to know whether it is the exception or the rule in *Pycnonotus*. There is almost as much distinctiveness and diversity in the food-calls and the birds' actions as there is in the mouth-patterns. The soft long-drawn "pwee pwee" of young *Chalcopelia afra* (least relished of all our Doves), compared by my wife to the very distant call of a Gull; the loud musical trill, like a cricket or tree-frog, of young *Macronyx croceus*; the wheeze of *Centropus*; the rather bell-like squeak of a *Coliuspasser*; and the rather short pleasing note, hard to describe but differing from all the above, of *Cisticola natalensis*, are examples. The marked differences between them can, at first sight, serve no very useful purpose in relation to the parent bird, though the mere fact that the species, and the adult call-notes, are different might

sufficiently account for most of them; but they are likely enough to be useful in "reminding" enemies, and I am inclined to think that there is quite a mnemonic element in some of these calls and displays. I am unable to refrain from quoting Mr. Bates' description of the behaviour of five young Kingfishers, *Alcedo guentheri* ('Ibis,' 1911, p. 515):—"While they remained alive for a few hours in a box, one of them continually made a most curious noise, something between a rattle and a fizzle, rhythmically varied in loudness by the opening and closing of the bill. Only one bird did this, and always the same one, while the rest remained silent. When that one was removed another, after some minutes, took up the *rôle* of 'soda-water bottle,' and when *that* one was removed *another* commenced. There was always one '*fizzler*' only."

In the external appearance of nestlings one also comes across many instances of moderate and a few of strong, even conspicuous, distinctiveness. Such are the special ornaments of the young Coot and Great Crested Grebe; the extraordinary general appearance of the nestling of the Lark-heeled Cuckoo, *Centropus burchelli*, quite black with sparse thread-like hairs of purest white (the down feathers) all over the upper surface; and, Mr. Wallis suggests, "the intense hairy blackness of the nestling in down of the Water-Rail. This is so conspicuous that it must have a cause, for it is not protective as is the marking of the Snipe in down." He goes on to mention its "fair" resemblance to "the larva of the Cream-spot Tiger-moth, which feeds on comfrey in the same marsh"*.

* It is interesting to quote the rest of the passage:—"The half-grown Lapwing, just when his back is getting green, but whilst tufts of down are still on him, is a most repulsive object. He lies about openly among the cows in a pasture and mimics a mass of wet, green excrement in which the mould is beginning to sprout, so exactly that nineteen people out of twenty would not touch him. Of course you know the immense yellow gape of the nestling Cuckoo, and his toad-like appearance. Country children have been afraid to touch one. . . . . You know the intense, hairy blackness, &c."

Quite possibly, in such cases as the Grebe and Coot, the conspicuous feature is often useful, as Mr. Pycraft suggests, as "a recognition mark, enabling the parents to find the young after they have dispersed into hiding to avoid an enemy"; but I cannot help suspecting that all these cases will probably be found to resemble the *Centropus* in the possession of some degree of nauseousness, and that the main factor in the selection of the distinctive features—or in their retention in the nestlings if they were originally selected in adult ancestors—will have been the need for differentiation by enemies from pleasanter geographically-associated species and a pleasanter parent-form, conformity with that necessity being brought about by mistaken attack and unmistaken refusal. On this view there is far less difficulty in accounting for ornamentation, not only in nestlings but throughout the animal kingdom, including those cases in which the possession of a conspicuous distinctive feature constitutes a departure from the rule of the genus or family, and for that other class of case, often quoted, in which two animals, be they adults, young, or eggs, are found exposed to the same environment and the same enemies and possessing similar habits: yet one is conspicuous, the other concealed.

Distinctiveness of a less marked order is less uncommon and, in naked nestlings, depends much on skin-colour. I have thought that blackness might be for protection from the sun. That this is not the only factor, if it be one at all, is shown by the fact that, at any rate in Africa, some of the blackest as well as of the least pigmented nestlings are found in covered nests. Both are also found in open nests. The influence of enemies will have to be invoked, I believe, to help us to, at any rate, a complete understanding of nestling appearance, and, incidentally, of some of the resemblances between unrelated nestlings. Those between Hawks and Owls and those between the members of some naked colour-groups are quite likely neither in their origin nor in their use entirely a matter of mimicry; yet the resemblances are

probably of much service in associating them in the minds of enemies, and this may have contributed to their selection.

4. Note on the Mouths of Adult Birds.

The mouths of adult birds are, in very numerous instances, quite as brilliant and striking as those of nestlings—often more so,—but in very few cases are they the same. After the young bird leaves the nest the mouth begins to alter, and at last takes on the full coloration of maturity. The old nestling combinations between different species have disappeared in the process, and new colour-associations are formed, to a far greater extent amongst unrelated birds than before. We have at Chirinda a black-mouthed combination, an orange-mouthed association, one with a yellow mouth with black extremities, another in which the yellow of the last is replaced by pink, yet another in which pink stands alone, and another which is entirely yellow. I will describe them all in greater detail later, and will figure members of some of the main associations to show what diverse and unrelated species have a similarly marked mouth when adult.

It may at first sight seem far-fetched, but I cannot help being convinced myself that the distinctive mouths of adult birds are explicable in much the same way as I have suggested for those of nestlings.

Everyone who has made a large collection of birds must have sometimes had the mortification of wounding one, and will have observed that a bird at bay, as a rule, holds its mouth open. I have had a good illustration of this. One night I was awakened by the fluttering of my birds in cages in the verandah. I went out. It was brilliant moonlight, and an Owl, *Syrnium woodfordi*, was swooping in at the cages. Stopped by the wire he each time wheeled round and stooped again. The occupants of the cages (insectivorous birds) were all down on the ground, terror-stricken, with their bills wide-open.

I feel that this unconscious display of the mouth-colours is equivalent to the final display of their concealed bright colours by so many insects when cornered and unable to escape. It is the last appeal to the enemy's memory, and the colour-groups I have referred to above are in some cases, I believe, in the nature of mimicry and "common warning colours."

Actually, there are three occasions on which a bird opens its mouth to an enemy—when a nestling, when at bay, and when mobbing. Even under the latter circumstances the display may conceivably be useful. But adult birds also sometimes show their mouths in ordinary intercourse and in courtship. I have seen this myself in Drongos and Hornbills, and it has been recorded for various sea-birds. Again, the female's mouth sometimes differs from the male's.

These two facts at once suggest, for the complete explanation of mouth-colours, the discussion of factors I have not yet touched on. They are best discussed with any real fullness under adult plumage and in connection with my detailed observational and experimental results from adult birds; but the brief discussion of one of them, and a short general statement of view, will be in place here, and the latter will help to preface my remarks on the coloration of eggs.

There is nothing new in the view that such sexual selection as would seem to take place is based, not necessarily on an admiration of the brightest suitors, but on a tendency to be attracted instinctively by masculine males and feminine females—according to the species, general standard of masculinity and femininity (which may or may not include brightness), and to fail to be thus attracted by atypical members of the species or of the opposite sex. But the instinct would be based, in turn, on the fact that atypical individuals and those showing the characters of the opposite sex are commonly specifically or sexually inefficient. Sexual selection might, therefore, be regarded both as a time-saver

for the fitter mates, and as one of several "tonic" factors that have themselves, perhaps, been selected for their burnishing effect on the specific and sexual characters that are actually useful in the struggle for existence and their accentuation of the general vigour and vitality of the species. The relationship thus suggested for vitality and ornamentation is one of common effect, not cause and effect. Other tonic factors, such as combat and persecution of the atypical, will, in many cases (as, apparently, in the Warblers), replace sexual selection wholly or in part, and the latter's complete or partial absence in these and other cases by no means proves its invalidity elsewhere. Elimination, again, may be indirect as well as direct. A female (or male) attracted now may already, by failing to be excited on former occasions, have relegated several potential mates to the greater likelihood of a poor or sterile match that will tend to result from delay; and discriminative coyness could produce selection of this less direct kind even where the sexes are equal in numbers.

This all brings us down to the view that display in courtship, though in many cases it has come to be modified and elaborated in special relation to courtship, is, in its essence, an exhibition of prowess or fitness in the various qualities—including distinctive coloration—that make for success in the everyday life of the species. That, in its origin, it had nothing to do with courtship, is suggested by the fact that the plumage-display, or mouth-display, of an animal at bay is often nearly identical with that of an animal courting, though without the added elaboration.

One such (perhaps unconscious) claim to fitness, in a character useful "in real life" mainly in relation to enemies, is probably represented by the mouth-display I have referred to just above. The fact that the coloration of the mouths was dull in the Hornbills, brilliant in the sea-birds (yet the same in both sexes), and somewhat different in the sexes of the Drongos, is in line with the fact that bright and dull plumage, plumage common to the sexes and plumage that is not so, is equally displayed in courtship; and both facts are

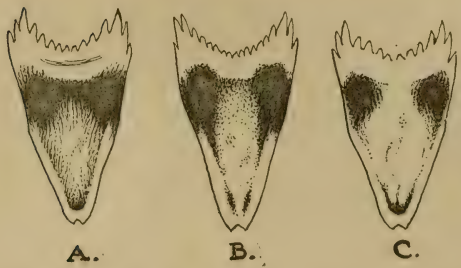
in full conformity with the view that the display in courtship is essentially an exhibition of specific and sexual efficiency.

Four years ago, I held the above view of sexual selection, but I did not regard it as likely, by itself, to make appreciable headway against the powerful factors that make for dullness, and I felt that bright colours and ornamentation could, perhaps, be sufficiently accounted for without it. But my later work, seeming for certain cases to eliminate alternative explanations and revealing unsuspected counteragents, convinced me that the selection of the *beau-idéal* may, under certain circumstances (as in the case of polygamy), have produced great results. I am unable, without it, to account to my satisfaction for the breeding-plumage of male *Pyromelana* and *Coliuspasser* among the birds best known to me in the field, and, as well as the reserve of males, a good contingent present here is in the habit of slipping down under the herbage when threatened.

I have gone into the question a little fully, on account of the striking use of the mouth-colours in courtship and also because we have, in the usually-closed mouth of a bird, so excellent a counteragent for brilliance within it that sexual selection might be expected to have here found a field for its accentuative operations. My adult mouths, since I took up mouth-coloration, have been mostly dry-season. Breeding-season mouths may or may not repay a special study.

Note.—Since writing the above I have come across several unusually reversionary tongues of nestling Warblers and *Pycnonotus*—the latter entirely instead of submarginally dusky as figured for this species and for *Macronyx*. These rather strongly suggest a derivation of the three-spot and twin-spot tongues from a generally dusky tongue. I figure three of such tongues among the Warblers (text-figure 6). The order is, of course, different from that suggested by the incomplete *Dryoscopus* series described above.

Text-figure 6.



Transitional nestling tongues. A and C, of *Prinia mystacea*, B, of *Cisticola cinerascens*, illustrating the evolution of the three-spot and the twin-spot tongues from, probably, a generally dusky tongue. The figures should be studied in conjunction with Mr. Collingwood Ingram's ('Ibis,' Oct. 1907, p. 575). The continued presence of scattered black-pigment cells, even on the cleared portion of the tongue, is interesting, as is their linear arrangement in the *Prinia*.

Another interesting point, previously overlooked, is Mr. Bates' observation to the effect that *Cisticola erythrops*, even when adult, never loses the twin spots. Both observations have a possible bearing on the question, Are the spots a nestling adaptation? and the first may be used as an argument in favour of that view, seeing that some (but not all) of the mouths concerned turn black again when the nestling stage is over.

EXPLANATION OF PLATE VII.

Fig. 1. *Amblyospiza albifrons*, mouth of nestling.

Fig. 2. *Coliuspasser ardens*, mouth of nestling. Fig. 3. Mouth of adult.

Figs. 4 and 4 *a*. *Lagonosticta rhodopareia*, nestlings. Fig. 4 *b*, mouth of adult. Fig. 5, mouth of young.

Fig. 6. *Cisticola natalensis*, mouth of fledged nestling; 6 *a*, of younger nestling; 6 *b*, tongue only of intermediate stage (for adult see fig. 12).

Fig. 7. *Estrilda astrild*, head of nestling.

Fig. 8. *Prinia mystacea*, mouth of nestling; 8 *a*, of adult; 8 *b*, of intermediate stage.
Fig. 9. *Chloropeta natalensis*, mouth of nestling (for adult see fig. 33).
Fig. 10. *Cisticola cinerascens*, nestling just hatched. Fig. 11, mouth of adult.
Fig. 12. *Cisticola natalensis*, mouth of adult (nestling, fig. 6).
Fig. 13. *Hyphantornis jamesoni*, mouth of nestling (adult, fig. 18).
Fig. 14. *Chrysococcyx* sp., mouth of nestling found with no. 13.
Fig. 15. *Pycnonotus layardi*, mouth of nestling (adult, fig. 38).
Fig. 16. *Lanius humeralis*, mouth of nestling (adult, fig. 47).
Fig. 17. *Colius striatus minor*, mouth of nestling; 17 *a*, of adult.
Fig. 18. *Hyphantornis jamesoni*, mouth of adult (nestling, fig. 13).
Fig. 19. *Macronyx croceus*, mouth of nestling. Fig. 20, of adult.
Fig. 21. *Centropus burchelli*, mouth of nestling.
Fig. 22. *Cinnyris venustus niassæ*, mouth of adult. Fig. 23, of nestling.
Fig. 24. *Chalcopelia afra*, part of mouth of nestling.
Fig. 25. *Turtur capicola damarensis*, mouth of nestling.
Fig. 25 *a*. *Dryoscopus guttatus*, mouth of nestling just hatched; 25 *b*, tongue of immature; 25 *c*, of adult ♀; 25 *d*, of adult ♂.
Fig. 26. *Turdus viscivorus*, mouth of nestling.
Fig. 27. *Turdus libonianus tropicalis*, mouth of adult.
Fig. 28. *Sigmodus tricolor*, mouth of adult.
Fig. 29. *Campephaga nigra*, mouth of adult ♂.
Fig. 30. *Alauda arvensis*, mouth of nestling.
Fig. 31. *Telephonus senegalus*, mouth of adult.
Fig. 32. *Crateropus kirki*, mouth of adult.
Fig. 33. *Chloropeta natalensis*, mouth of adult (nestling, fig. 9).
Fig. 34. *Laniarius* sp., mouth of adult.
Fig. 35. *Bradiornis murinus*, mouth of adult.
Fig. 36. *Trochocercus albonotatus swynnertoni*, mouth of adult.
Fig. 37. *Dicrurus ludwigi*, mouth of adult.
Fig. 38. *Pycnonotus layardi*, mouth of adult (nestling, fig. 15).
Fig. 39. *Phyllostrophus flavistriatus*, mouth of adult.
Fig. 40. *Anthus pyrrhonotus*, mouth of adult.
Fig. 41. *Trochocercus* sp., mouth of adult.
Fig. 42. *Trachyphonus cafer*, mouth of adult (¾ nat. size).
Fig. 43. *Rhinopomastus cyanomelas*, mouth of adult.
Fig. 44. *Trachyphonus cafer*, tongue of an immature.
Fig. 45. *Irrisor erythrorhynchus*, mouth of adult ♂.
Fig. 46. *Vinago delalandei*, mouth of adult.
Fig. 47. *Lanius humeralis*, mouth of adult (nestling, fig. 16).